

INFRAGENERIC TAXONOMY OF *ASTROPHYTUM* (CACTACEAE), WITH REMARKS ON THE STATUS OF *DIGITOSTIGMA*

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ABSTRACT

In a monograph of the genus *Astrophytum*, Megata (1944) proposed two infrageneric sections—*Astrophytum* sect. *Austrastrophytum* and *A. sect. Septentriastrophytum*. *Astrophytum* sect. *Austrastrophytum* which contains the type of the genus is in violation of Art. 22.2 of the ICBN which requires that a name of a subdivision of a genus that includes the type of that genus repeat as its epithet the generic name unaltered. Backeberg (1950) proposed two subgenera: *Astrophytum* subg. *Euastrrophytum* and *A. subg. Neoastrophytum*, which essentially corresponded to Megata's sections. However, Backeberg's *A. subg. Euastrrophytum*, containing the type species of the genus, violated Art. 22.2 and Art. 21.3 of the international code.

In 1961, Backeberg used *Astrophytum* subg. *Neoastrophytum* in his treatment of the genus, but proposed *Astrophytum* subg. *Astrophytum* to replace *A. subg. Euastrrophytum*. Therefore, Backeberg's (1961) subgeneric names are valid, and have received wide circulation, and should be accepted; Megata's two sections should be suppressed. On the basis of comparative flower and fruit morphology, the species *Digitostigma caput-medusae* Velazco & Nevárez appears to have evolved within the genus *Astrophytum*, and shows a closer relationship to *A. subg. Neoastrophytum* than to *A. subg. Astrophytum*. However, because of its aberrant characteristics (tuberculate habit, dimorphic areoles, large, fusiform root, and nearly circular seeds with an acute basal cleft and verrucose testa), *caput-medusae*'s placement in *Astrophytum* subgenus *Stigmatodactylus* D. Hunt appears justified, though provisional, because its status as an ancient generic hybrid remains a possibility. Molecular genetic studies are needed to further clarify the evolutionary relationships of *A. caput-medusae*.

RESUMEN

En una monografía del género *Astrophytum*, Megata (1944) propuso dos secciones infragenéricas —*Astrophytum* sect. *Austrastrophytum* y *A. sect. Septentriastrophytum*. *Astrophytum* sect. *Austrastrophytum* que contiene el tipo del género viola el Art. 22.2 del ICBN que requiere que un nombre de una subdivisión de un género que incluya el tipo del género repite como epíteto el nombre genérico inalterado. Backeberg (1950) propuso dos subgéneros: *Astrophytum* subg. *Euastrrophytum* y *A. subg. Neoastrophytum*, que esencialmente corresponden a las secciones de Megata. Sin embargo, *A. subg. Euastrrophytum* Backeberg, contiene la especie tipo del género, y viola los Art. 22.2 y Art. 21.3 del Código internacional.

En 1961, Backeberg usó *Astrophytum* subg. *Neoastrophytum* en su tratamiento del género, pero propuso *Astrophytum* subg. *Astrophytum* para reemplazar *A. subg. Euastrrophytum*. Por tanto, los nombres subgenéricos de Backeberg (1961) son válidos, han tenido amplia circulación, y deben ser aceptados; las dos secciones de Megata deben suprimirse. En base a la morfología comparativa de flor y fruto, la especie *Digitostigma caput-medusae* Velazco & Nevárez parece haber evolucionado en el género *Astrophytum*, y muestra una relación más grande con *A. subg. Neoastrophytum* que con *A. subg. Astrophytum*. Sin embargo, debido a sus características aberrantes (hábito tuberculado, areolas dimórficas, raíz ancha, fusiforme, y semillas casi circulares con una hendidura basal y testa verrucosa), el emplazamiento de *caput-medusae* en *Astrophytum* subgénero *Stigmatodactylus* D. Hunt parece justificado, aunque provisional, porque su estatus como un antiguo híbrido genérico es aún una posibilidad. Se necesitan estudios genéticos moleculares para clarificar las relaciones evolutivas de *A. caput-medusae*.

SUBGENUS VS. SECTION

The cactus genus *Astrophytum* comprises a small group of species occurring principally in the Chihuahuan Desert region of central and northern Mexico, with one species entering southern Texas (Anderson 2001; Hunt et al. 2006). On the basis of hybridization experiments involving the different species, Möller (1927) recognized two apparently natural groups within the genus. A decade later, the German horticulturalist, Curt Backeberg (1937), presented a brief, descriptive key to the species of *Astrophytum* in *Blätter für Kakteenforschung*, a bulletin of cactus research. He also recognized two groups within the genus—Group A having apical fruit dehiscence and yellow flowers, and Group B with basal fruit dehiscence and red-throated flowers.

Moritane¹ Megata, a student of horticultural sciences at the Kyoto Imperial University in Kyoto, Japan,

¹Moritane, not Molitane is the correct spelling of Megata's first name; see Hoock (2008, p. 248) for explanation.

published the first monographic treatment of the genus *Astrophytum* in 1944. Data from experimental hybridization and comparative morphology, led him to propose two infrageneric sections—*Astrophytum* sect. *Septentriastrophytum* (diagnosis: *Flores floribus Sect. Austrastrophyti majores, aurea praeter intus basi rubra; fructus carnosus, irregulariter dehiscens; semina copiosa, 80–300, nigra vel luteobrunnescentia.*), and *A.* sect. *Austrastrophytum* (diagnosis: *Flores minores quam flores Sect. Septentriastrophyti, lutei et non rubric intus ad basim; fructus siccus, stellatim dehiscens; semina 40–60, nigra*). Megata recognized five species, placing *A. myriostigma* and *A. ornatum* in *A.* sect. *Austrastrophytum* and *A. asterias*, *A. capricorne*, and *A. coahuilense* in *A.* sect. *Septentriastrophytum*.

In 1950, Curt Backeberg published two subgenera under *Astrophytum* which corresponded exactly to Megata's (1944) sections. He proposed *Astrophytum* subg. *Euastrophytum* (diagnosis: *Fauce lutea; fructu apice stellariter dissiliente*) with the type species *Astrophytum myriostigma* Lem. (1839) and *A.* subg. *Neoastrophytum* (diagnosis: *Fauce rubra; fructu basi dissiliente*), with the type species *Echinocactus asterias* Zuccarini (1845).

Backeberg's six volume series *Die Cactaceae* was published in 1958 to 1962, and the genus *Astrophytum* was treated in his volume 5 (1961). Backeberg proposed *Astrophytum* subg. *Astrophytum* to replace *A.* subg. *Euastrophytum*, and adopted his previously published *A.* subg. *Neoastrophytum*. He apparently realized that *Astrophytum* subg. *Euastrophytum* violated Art. 22.2 of the ICBN which requires that a name of a subdivision of a genus that includes the type of that genus repeat as its epithet the generic name unaltered, and therefore this subdivision should have been named *Astrophytum* subg. *Astrophytum*. Furthermore, Art. 21.3 forbids the epithet of a subdivision of a genus to be formed from "Eu" plus the generic name. Backeberg separated the two subgenera on the basis of fruit morphology, type of fruit dehiscence, and seedling color. He recognized a total of six species, placing *A. myriostigma* and *A. ornatum* in *Astrophytum* subg. *Astrophytum*, and *A. asterias*, *A. capricorne*, *A. coahuilense*, and *A. senile* in *A.* subg. *Neoastrophytum*. He followed the same taxonomy in the first (1966), second (1970) and third (1976) editions of *Kakteenlexikon* (as well as the English version of the third edition, *Cactus Lexicon* 1977). However, he abbreviated the subgeneric diagnoses, using only the mode of fruit dehiscence as a diagnostic trait.

The fundamental dichotomy within the genus *Astrophytum* was also recognized by the *Astrophytum* specialist Otakar Sadořský who carried out long-term hybridization experiments involving hundreds of plants. However, he and his coauthors did not give formal taxonomic recognition, either at the level of section or subgenus, to these two clades (Haage & Sadořský 1957; Sadořský & Schütz 1979). More recent evidence from chloroplast DNA seems to further support this basic division within *Astrophytum* (Wallace 1995, Fig. 5).

As is evident from the foregoing discussion, essentially the same two groups of species in the genus *Astrophytum* have been treated in the past both as sections and as subgenera by two different authors, creating a taxonomic problem requiring resolution. Furthermore, this problem has persisted in recent works. In *The New Cactus Lexicon* (Hunt et al. 2006: 31), Backeberg's *Astrophytum* subg. *Astrophytum* and *A.* subg. *Neoastrophytum* are recognized as well as *A.* subg. *Stigmatodactylus* D. Hunt. By contrast, in a new monographic treatment of *Astrophytum*, Hooek (2008) allocates five species to Megata's (1944) sections, *A.* sect. *Austrastrophytum* and *A.* sect. *Septentriastrophytum*, and places a sixth species, *Astrophytum caput-medusae* (Velazco & Nevárez) D. Hunt, in *A.* subg. *Stigmatodactylus* D. Hunt, following Hunt (2003a, b).

The decision whether to divide a genus into sections or subgenera is subjective. In reviewing the question in this case, it appears that the use of the subgenus is more appropriate and justifiable than the use of the section for the following three reasons: 1) Megata's (1944) *A.* sect. *Austrastrophytum* is in violation of ICBN Art. 22.2 because this section includes the type (*Astrophytum myriostigma*) of the generic name; it should have been named *A.* sect. *Astrophytum*. 2) Backeberg's two subgeneric names, *A.* subg. *Astrophytum* and *A.* subg. *Neoastrophytum*, are validly published and have received wide circulation, appearing in volume 5 of his *Die Cactaceae* and in all three German editions of *Kakteenlexikon* as well as the English translation of his third edition. 3) Hunt (2003a, b) proposed *A.* subg. *Stigmatodactylus* to accommodate the morphologically divergent *A. caput-medusae*, thereby setting further precedence for the use of the subgenus category as opposed to the section, and as indicated above, the subgenus category was adopted in *The New Cactus Lexicon*.

STATUS OF *DIGITOSTIGMA*

Velazco and Nevárez (2002) described a new genus and species, *Digitostigma caput-medusae* from Nuevo León, Mexico. Subsequently, Hunt (2003a) wrote: “The authors of *Digitostigma caput-medusae* are to be congratulated on a truly remarkable discovery, but the feeling of our group is that its peculiar habit is not sufficient in itself to justify excluding it from *Astrophytum*, with which it shares unusual and significant features in common, i.e., the floccose indumentum and eccentric (hat-shaped) seeds, as well as having very similar flowers.” Hunt (2003a) therefore placed *Digitostigma* in the synonymy of *Astrophytum* and recombined the species as *Astrophytum caput-medusae* D. Hunt.

Shortly thereafter, Hunt (2003b) wrote that Kanchi Gandhi of Harvard University had determined that Velazco and Nevárez “had failed to indicate the type of the generic plant in the explicit manner required for the ICBN,” thus invalidating both the name *Digitostigma* and the species name. Gandhi regarded Hunt (2003a) as the valid publication of the name *Astrophytum caput-medusae* as well as the subgeneric name, *A. subg. Stigmatodactylus*. But according to Hunt (2003b), Nigel Taylor argued that Velazco and Nevárez had failed to provide a validating Latin diagnosis for the species name and therefore the original description and Hunt’s revision were invalid. To correct this error, Hunt (2003b) published a second formal revision as follows:

“*Astrophytum caput-medusae* D. Hunt *ab aliis speciebus generic Astrophyti caule tuberculis elongates areolis bipartitis maxime differt*. Type: Mexico, edo. Nuevo León, [locality withheld], matorral espinoso tamaulipeco, 100–200 m, 28 Aug 2001, Nevárez & Velazco s.n. (UNL 023704 holo.; UNL 023705 iso.). Syn: *Digitostigma caput-medusae* Velazco & Nevárez, *Cact. Suc. Mex.* 47(4):81–82 (2002) nom inval. (Art. 43.1).”

“*Astrophytum subg. Stigmatodactylus* D. Hunt Replaced *Digitostigma* Velazco & Nevárez *Cact. Suc. Mex.* 47(4):79 (2002) nom inval. (Art. 37.5), quoad descr. Lat. Type: *Astrophytum caput-medusae* D. Hunt.”

Then in the editorial section of *Cactaceae Systematics Initiatives* 20:4. 2005, we are informed that Roberto Kiesling and Detlev Metzger proposed a clause to ICBN Art. 37, that was approved by the International Botanical Congress in Vienna (July 2005). The clause removes the “pitfall” introduced when said Article was previously amended in 1990 which invalidated the generic name *Digitostigma* Velazco & Nevárez when originally published, as well as the specific names *D. caput-medusae* Velazco & Nevárez and *Astrophytum caput-medusae* (Velazco & Nevárez) D. Hunt. The draft Art. 37.7 states: “In the case of a new monotypic genus (or monotypic infrageneric taxon above the rank of species), the correct mention of, or reference to, the type of the species name is sufficient.” As a result of the acceptance of the clause to Art. 37, the original names in *Cactaceas y Suculentas Mexicanas* 47(4):76–86. 2002, and the recombination in *Astrophytum* (*Cactaceae Systematics Initiatives* 15:6. 2003a) retroactively became validly published, and the “validation” of *A. caput-medusae* (*Cactaceae Systematics Initiatives* 16:4. 2003b) was judged superfluous. Consequently, if authors prefer to classify the new taxon as a distinct genus, the correct name would be *Digitostigma caput-medusae* Velazco & Nevárez. But if it is to be regarded as a member of *Astrophytum*, then the correct name would be *Astrophytum subg. Stigmatodactylus caput-medusae* (Velazco & Nevárez) D. Hunt, and *Digitostigma* would be placed in the synonymy of *Astrophytum*.

Detailed morphological comparisons between *caput-medusae* and *Astrophytum* have been lacking until now. In an attempt to clarify *caput-medusae*’s affinities and generic status, a summary of my comparative study is presented below. Flowers, fruits, and seedlings of the following taxa were examined (number of flowers, fruits, adult plants, and seedlings in parentheses): *A. ornatum* (3, 3, 2, 69), *A. myriostigma* (22, 41, 41, 249), *A. asterias* (29, 5, 5, 59), *A. capricorne* (40, 11, 14, 82), *A. coahuilense* (16, 20, 20, 120), and the species *caput-medusae* (34, 8, 5, 14).

The flower of *caput-medusae* has a vivid orange color at the base of the inner perianth segments (Velazco & Nevárez 2002) and in this respect it is similar to that of *A. subg. Neoastrophytum* species in which the inner perianth segments vary from crimson to orange. By contrast, members of *A. subg. Astrophytum* have entirely yellow flowers. The fruit of *A. subg. Neoastrophytum* is described as fleshy and turns pink, red, or reddish purple when ripe, whereas that of *A. subg. Astrophytum* is less fleshy and remains green (Megata 1944; Hooek 2008). The fruit of *caput-medusae* is similar to that of *A. subg. Neoastrophytum* in that it usually

turns pink at maturity (Hooek 2008); but at maturity it appears less fleshy to nearly dry and in this respect is similar to the fruit of *A.* subg. *Astrophytum*. The fruit of *caput-medusae* undergoes longitudinal dehiscence (Velazco & Nevárez 2002) and hence differs from both *Astrophytum* subgenera. According to Velazco and Nevárez (2002:82), the remains of the perianth are deciduous and leave a 3 mm diameter scar. However, in all fruit that I observed the floral remnants persisted until dehiscence. In *A.* subg. *Neoastrophytum* the floral remnants are strongly attached to the fruit, but in *A.* subg. *Astrophytum* they usually detach from the fruit at the time of dehiscence, leaving a small scar.

The flower and fruit of *caput-medusae* display similarities in particular with those of *Astrophytum asterias*. In both taxa, the exterior perianth segments are greenish-yellow and they usually lack, or have few, black tips. In *A.* subg. *Neoastrophytum capricorne* and *A.* subg. *Neoastrophytum coahuilense* the exterior perianth segments are usually yellow with black tips, and often there is a reddish line or spot near each black tip. The bases of the inner perianth segments in *caput-medusae* are vivid orange; in *A. asterias* the color may vary from dark red to pink or orange. In *A. capricorne* and *A. coahuilense*, the bases of the inner perianth segments are usually dark crimson, but may vary from pale red to orange, or rarely, pure yellow in natural populations (Hooek 2008). In *A. asterias* the mature fruit turns pink (Hooek 2008; this study) like that of *caput-medusae*. Furthermore, in *caput-medusae*, the receptacle tube and pericarpel are covered with fewer lanceolate scales and more white wool than in the species of both *Astrophytum* subgenera, except in *A. asterias* which displays a further reduction in number and size of these scales (i.e., spinescent bracteoles) and more wool, especially on the pericarpel.

Velazco and Nevárez (2002) stated that the seeds of *D. caput-medusae* are “hat-shaped” and compare favorably with those of *Astrophytum*, and according to Hunt (2003a) they resemble those of *A. asterias*. However, my study suggests that the seeds of all *Astrophytum* species are very similar to one another and differ collectively from those of *D. caput-medusae* in several ways. The seeds of all *Astrophytum* species have a smooth testa whereas those of *D. caput-medusae* are verrucose (Velazco & Nevárez 2002). The seeds of *Astrophytum* clearly fit the concept of “hat-shaped,” with a peaked, but rounded profile opposite the hilum and a rather flat base (where the concavity of the hilum is situated). But the seeds of *caput-medusae* have a deeply and acutely angled cleft at the concavity of the hilum and the lateral profile opposite the hilum is especially enlarged and rounded.

The seedlings of *caput-medusae* are usually light green, but they can be dark violet in color. Seedlings of all members of *A.* subg. *Neoastrophytum* are typically light green, whereas those of *A.* subg. *Astrophytum* are generally russet or reddish brown, rarely green.

The distributional relationships of the taxa under consideration are also informative. *Astrophytum* subg. *Astrophytum* has a southerly distribution with *A. myriostigma* centered on the plateau of San Luis Potosi and adjacent areas including the Jaumave Valley, and *A. ornatum* occurring through the barranca region as far south as the state of Hidalgo (Megata 1944; Hooek 2008). On the other hand, *A.* subg. *Neoastrophytum* has a northerly distribution, ranging from extreme northern Zacatecas and adjacent Durango, northward and eastward through Coahuila and adjacent Nuevo León into southern Texas (Hooek 2008). The species *caput-medusae* also has a northern distribution, being restricted to northern Nuevo León (Velazco & Nevárez 2002) adjacent to the range of *A. capricorne* and *A. asterias*.

In sum, comparative data from flower and fruit characteristics, and seedling color support the hypothesis that *caput-medusae* is a member of the genus *Astrophytum*. Moreover, the evidence (including geographic relationships) suggests that *caput-medusae* is more closely related to *A.* subg. *Neoastrophytum* than to *A.* subg. *Astrophytum* and may have evolved from the former group after it had separated from the latter. Therefore, accepting *Digitostigma* as a distinct genus to accommodate *caput-medusae* would render the genus *Astrophytum* a paraphyletic taxon, which would be undesirable in a classification system based on phylogenetic principles. It is clear, however, that *caput-medusae* has undergone considerable morphological divergence from the other *Astrophytum* species, possibly as a result of strong selection pressures for adaptation to the Tamaulipan thornscrub habitat, perhaps as a shrub debris mimic.

As an alternative hypothesis, the remarkable divergence resulting in the unusual suite of morphological characteristics (tuberculate habit, dimorphic areoles, large, fusiform root, and large rounded seeds with a verrucose testa and acute basal cleft) could be explained by intergeneric hybridization, a possibility previously raised by Hunt (2003a). If true, separate generic status for *caput-medusae* would then be justified. If *caput-medusae* is an ancient hybrid, it is reasonable to assume that a member of *A.* subg. *Neoastrophytum* was involved as one of its parents. The other parent could have had a pure yellow flower. One characteristic of the flower of *caput-medusae* that suggests hybridization is the narrowness of zone of orange color surrounding the stamens. A narrow zone of color is typical of *Astrophytum* hybrids produced artificially by crossing a pure yellow-flowered species (e.g., *A. myriostigma*) with a species with red-throated flowers (e.g., *A. capricorne*, *A. asterias*); see Hoock (2008) for examples. Without doubt, molecular genetic studies are needed to further clarify the evolutionary relationships of *caput-medusae*.

CONCLUSIONS

It is recommended that *A.* sect. *Austrastrophytum* Megata nom. inval., (Art. 22.2), and *A.* sect. *Septentriastrophytum* Megata should be suppressed. Backeberg's *Astrophytum* subg. *Astrophytum* and *A.* subg. *Neoastrophytum* should be accepted and used when necessary. The species *Digitostigma caput-medusae* Velazco & Nevárez appears to have evolved within the genus *Astrophytum*, and shows a closer relationship to *A.* subg. *Neoastrophytum* than to *A.* subg. *Astrophytum*. However, because of its aberrant morphology, *caput-medusae*'s placement in *A.* subg. *Stigmatodactylus* D. Hunt appears justified, though provisional; its status as an ancient intergeneric hybrid remains a possibility. Molecular genetic studies are needed to resolve this question. Protologues and a diagnostic key to the three subgenera follow:

Astrophytum* subg. *Astrophytum Backebg., *Die Cactaceae* 5:2655, fig. 2526, 1961. Subg. *Euastrrophytum* Backebg., *Cac. Succ. J.* (Los Angeles) 22:5. 154. 1950. TYPE SPECIES: *Astrophytum myriostigma* Lem., *Cact. Gen. Sp. Nov.* 4(-6). 1839. TYPE LOCALITY: not cited.

Diagnosis.—Fauce lutea; fructu apice stellariter dissiliente. *Distribution.*—North-central Mexico (Backeberg 1950:154).

Diagnosis.—Frucht sternformig aufspringend, mit festerer Wand, Samlinge rotbraun (Backeberg 1961:2653).

Note.—Distribution is central Mexico, not north-central Mexico.

Astrophytum* subg. *Neoastrophytum Backebg., *Cac. Succ. J.* (Los Angeles) 22:5. 154. 1950. TYPE SPECIES: *Echinocactus asterias* Zucc., *Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss.* 4(2):13, t. 3. 1845. TYPE LOCALITY: Mexico.

Diagnosis.—Fauce rubra; fructu basi dissiliente. *Distribution.*—Central Mexico.

Note.—Distribution is north-central Mexico, not central Mexico.

Astrophytum* subg. *Stigmatodactylus D. Hunt, *Cactaceae Syst. Init.* 15:6. 2003. REPLACED SYNONYM: *Digitostigma* Velazco & Nevárez, *Cact. Succ. Mex.* 47:79. 2002. TYPE: *Digitostigma caput-medusae* Velazco & Nevárez, *Cact. Suc. Mex.* 47:81–82.

'*Digitostigma*' not only contravenes Linnaean canons for the formation of generic names but implies that the plant is notable for its finger-shaped stigmas rather than its spotted tubercles, contrary to the authors' explicit intention. For this reason the opportunity afforded by the change of rank has been taken to provide an unambiguous name formed according to classical usage.

Astrophytum caput-medusae (Velazco & Nevárez) D. Hunt, *Cactaceae Syst. Init.* 15:6. 2003. *Digitostigma caput-medusae* Velazco & Nevárez, *Cact. Suc. Mex.* 47:81–82. TYPE: MEXICO. NUEVO LEÓN: [locality withheld], matorral espinoso tamaulipeco, 100–200 m, 28 Aug 2001, Nevárez & Velazco s.n. (HOLOTYPE: UNL 023704; ISOTYPE: UNL 023705).

Diagnosis.—Radix fusiformis radices secundariis edens, pro ratione plantae parte aerea magna. Caulis brevis, cylindraceus, costas carens, tuberculis longissimis gecilibus ex caulis apice orientibus, epiderme stigmatibus obiecta. Spinae plerumque adsunt, in radiales vel centrales non differentes, breves, non perfecte rectae, aliquantum undulatae, albidae, ad apicem atrocastaneae. Areolae dimorphae: spinifera ad tuberculi apicem, albolanata, circularis; florifera adaxialis, in tuberculi parte subterminali, a spinifera disjuncta. Flores in tuberculorum parte subterminali evolventium, non apicales, diurni, flavi, peranthi segmentis interioribus base aurantiaca, segmentis exterioribus flavo-viridibus; tubo receptaculari squamis lanceolatis, papiraceis, arista terminali obiecto, in quorum axillis pilis brevibus albis parientibus; pericarpello isdem squamis munito. Fructus juvenis viridis, carnosus, squamis lanceolatis ad axillis lanatis, ad maturitate sicco, dehiscentia longitudinali irregulari. Semina magna (*Astrophyti* similia), ad 3 mm longa, pileata, testa tuberculata, nigra vel atrobrunnea; hilo basali profundissimo, micropyle ab hilo externo, sed ad id contiguo (Velazco & Nevárez 2002:79).

KEY TO SUBGENERA

1. Fruits remain green, open apically; flowers yellow _____ subg. **Astrophytum** Backebg. (*A. myriostigma*, *A. ornatum*)
1. Fruits turn pink, red or red-purple when ripe, split basally in circular fashion, disintegrate basally, or split longitudinally in irregular manner; flowers yellow usually with orange or red throat.
 2. Body with ribs _____ subg. **Neoastrophytum** Backebg. (*A. asterias*, *A. capricorne*, *A. coahuilense*)
 2. Body with elongate tubercles _____ subg. **Stigmatodactylus** D. Hunt (*A. caput-medusae*)

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